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THE ORIGIN AND EARLY EVOLUTION OF TURTLES

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■ **Abstract** A critical reexamination of turtle relationships continues to support a sister-group relationship of turtles with a clade of marine reptiles, Sauropterygia, within crown-group Diapsida (Sauria). The high Homoplasy Index raises concerns about the phylogenetic information content of various morphological characters in broad-scale phylogenetic analyses. Such analyses may also suffer from inadequate statements of primary homology. Several such statements that have played an important role in the analysis of turtle relationships (dermal armor, acromion, astragalo-calcaneal complex, hooked fifth metatarsal) are reviewed in detail. An evolutionary scenario for the origin of the turtle *bauplan* suggests an aquatic origin of turtles, which is supported not only by their sauropterygian relationships, but also by paleobiogeographic and stratigraphic considerations. However, turtle relationships remain labile, and further investigations of their relationships are required, involving molecular and physiological data.

INTRODUCTION

In a comprehensive evaluation of turtle relationships, Gregory (26) compared living and fossil turtles with placodonts, "cotylosaurs" (captorhinids, pareiasaurs, procolophonoids, and diadectomorphs, all considered amniotes at the time), and with seymouriamorphs. He concluded that Testudines were derived from Paleozoic "cotylosaurs," and that among those, pareiasaurs approached Triassic turtles more closely than the geologically older diadectids. Although placodonts, especially *Henodus*, had evolved an amazingly turtle-like appearance, Gregory concluded that they were not related to turtles and that convergent evolution, especially related to dermal armor, causes a serious problem in recognizing testudine relationships.

Olson (52) reconsidered the origin of turtles as part of a reevaluation of Paleozoic and Mesozoic amniotes. He argued for a basic division of amniotes into Parareptilia and Eureptilia, and he suggested a derivation of turtles from basal parareptiles, i.e., the diadectids. Much later, Carroll (9) proposed an origin of turtles from among basal captorhinids. The advent of cladistics caused a major shift in ways of looking at turtle origins. The first large-scale computer-assisted phylogenetic analysis of amniote relationships (20) supported turtle relationships with captorhinids. Two other important results of this analysis were the exclusion of diadectomorphs from amniotes, and the recognition of a clade of parareptiles including mesosaurs, millerosaurs, pareiasaurs, and procolophonoids. Monophyly of this clade was poorly supported, however, mainly because of lack of detailed anatomical information about its members.

Largely as a response to this paper, Reisz & Laurin (58) proposed an alternative hypothesis of relationships, i.e., that turtles were nested within parareptiles, closely related to procolophonoids. This result was based, in part, on the study of *Owenetta*, a basal procolophonian that shares a suite of synapomorphies with turtles. By contrast, the study of pareiasaurs led Lee (39) to conclude that they, rather than procolophonoids, are the closest known relatives of turtles. Subsequently, Laurin & Reisz (38) incorporated the new anatomical data on pareiasaurs presented by Lee (39) into their own analysis, but they continued to find support for the hypothesis of procolophonoid-turtle relationships. However, possible turtle relationships were constrained in this analysis because, other than parareptiles and captorhinids, it included only basal diapsids and basal synapsids for possible comparison. A second, slightly later publication by Lee (41) included previously withheld anatomical data that again turned turtle relationships to pareiasaurs. However, Lee's (41) analysis constrained turtle relationships even more seriously because the choice of terminal taxa was based on the a priori assumption that turtles are, indeed, parareptiles.

Continuing controversy over turtle relationships (42, 66) culminated in two adjoining articles in a single issue of the *Zoological Journal of the Linnean Society* (43, 11). Lee (43) now included most pareiasaurs as terminal taxa, with the result that turtles were found to be nested within pareiasaurs, as sister-taxon to the poorly known yet derived genus *Anthodon*. DeBraga & Rieppel (11) pursued a global approach instead by including representatives of most Paleozoic and early Mesozoic amniote taxa in order to test for patterns of turtle relationships among a broad array of amniotes. As a result of their analysis, deBraga & Rieppel (11) proposed a highly controversial hypothesis, i.e., that turtles are nested within diapsids as sister-group of a clade of Mesozoic marine reptiles, the Sauropterygia. It is the latter hypothesis that we propose to reexamine in this review by modifying the data set in accordance with recent criticisms (44) and with other recent increases in our knowledge of the relevant taxa, and by reanalyzing the data using the software packages PAUP version 3.1.1. (74) and McClade version 3 (47).

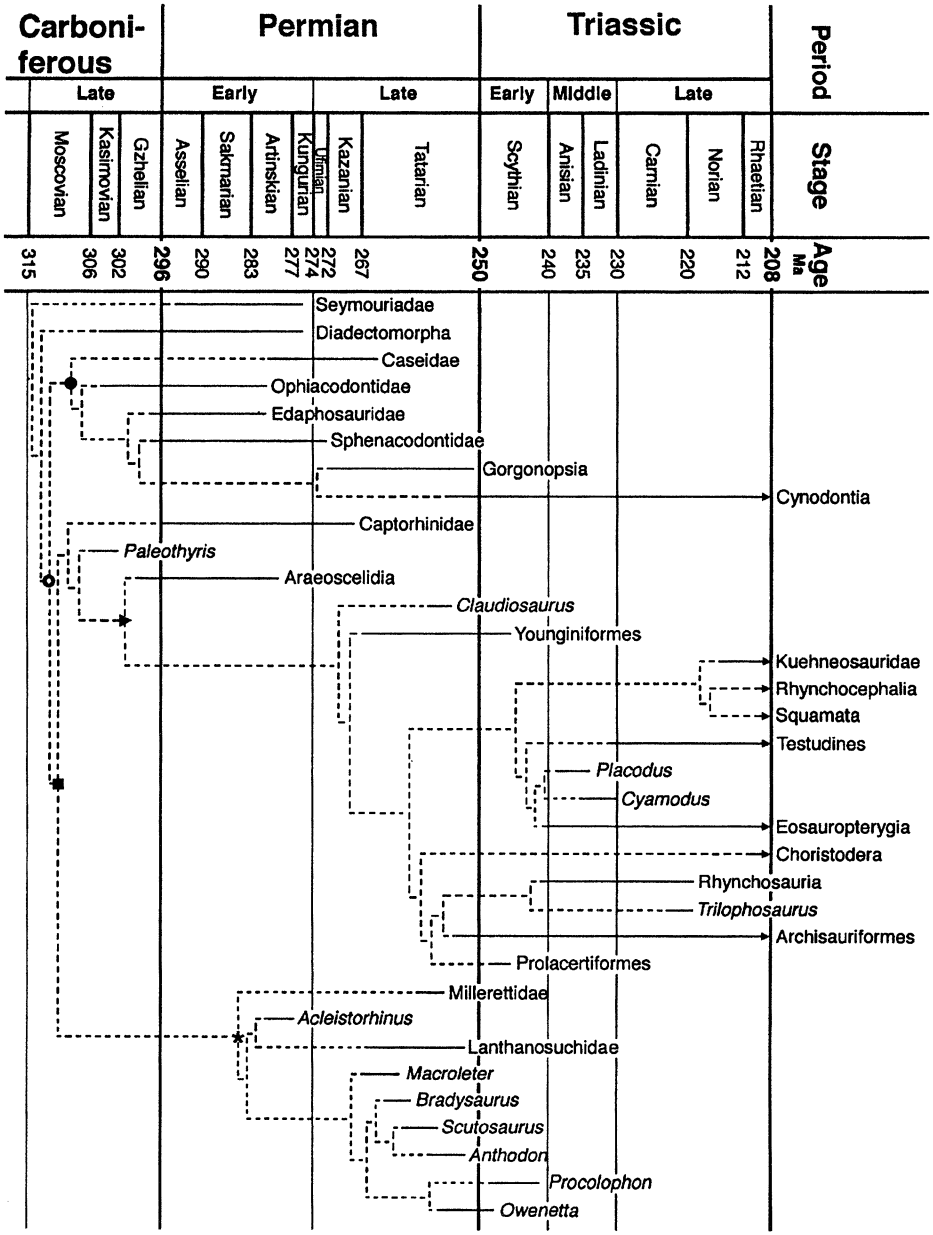
CHANGES TO THE GLOBAL DATA MATRIX

Lee (44) examined the data matrix of deBraga & Rieppel (11, 66) and argued that many of the characters were incorrectly coded. We have examined the proposed corrections and agree with the majority (the characters are numbered as in the above two papers: 44–46, 70, 73, 77, 87, synapsid part of 120, 124, 126, 150, 160, and 164). Changes were incorporated in the present study in accordance with Lee's (44) interpretations. However, we disagree with several of the proposed corrections, and for these retain the original coding. They include: [65] distinct basal tubera are absent in pareiasaurs, which show a secondarily derived condition, i.e., basal tubera on the parasphenoid; [82] the position of the mandibular joint relative to occiput is polymorphic in turtles; [103] cervical centra of pareiasaurs are ridged but not keeled; [120, 121] one coracoid ossification is present, and the coracoid foramen is enclosed by the coracoid and scapula, in pareiasaurs; [127] the presence of the ectepicondylar foramen in the humerus is polymorphic for turtles; [140] a weak 4th trochanter is present in pareiasaurs and shifted to the edge of the femur; [152] the first distal tarsal is retained as polymorphic in turtles.

We also reexamined the data matrix published by deBraga & Rieppel (11) as part of our attempt to identify possible biological causes for apparent patterns of character conflicts in their phylogeny. This effort resulted in the following changes of character coding: Character 69 (occipital flange of parietal) has been almost entirely recoded, taxa 1–14 and 20–22 all having this feature (1), which is sometimes covered posteriorly by other elements such as the postparietal and tabular. *Paleothyris*: 139/0 → 1; Millerettidae: 125/? → 1; *Bradysaurus*: 80/1 → 0; 125/? → 0; 144/1 → 0; *Scutosaurus*: 80/1 → 0; 125/? → 0; 144/1 → 0; *Anthodon*: 80/1 → 0; 125/? → 0; 144/1 → ?; *Owenetta*: 52/0 → 0&2; Kuehneosauridae: 29/? → 0; 78/2 → 0; 125/0 → 1; Testudines: 83/0 → 1;142/0 → 1; 167/1 → 0&1; Rhynchocephalia: 68/0 → 0&1; *Placodus*: 41/? → 1; 64/1 → ?; 77/0 → 1; 83/1 → 1&2; 89/1 → 0; 112/? → 1; 140/0 → 1; 165/2 → 1; Eosauropterygia: 6/0 → 1; 31/1 → 0&1; 37/0 → 1; 41/? → 1; 59/2 → 1&2; 87/0 → 1; 97/? → 1; 112/0 → 0&1; 140/0&1 → 1; 142/0&1 → 1&2.

In addition, we decided to code the placodont *Cyamodus* to ensure that we can provide a proper test of the possibility that turtles are either nested within placodonts or that the striking similarities of cyamodontoid placodonts and turtles are, indeed, convergent. The following list represents the coding, in groupings of five, for all the characters listed in deBraga & Rieppel (1997): *Cyamodus* 10000 101(0&1)0 10000 0212? 00(0&1)0(0&1) 00001 00001 11110 1?00? ?0121 32212 01021 00??1 01101 01201 21201 21111 01000 ?1101 00?10 ??111 1111? 1111? 00010 11111 10121 ??1?0 01011 0?111 ??1?? 0???? ????? ?0002 000.

The resulting data matrix was reanalyzed using PAUP version 3.1.1. (74), implementing the same search procedures as in the original analysis (11). The results duplicate the tree topology of the original study (11, 66), with turtles nested within diapsids as the sister-group of sauropterygians (Figure 1). To ensure proper comparison of the phylogenetic analyses of Lee (43) and deBraga & Rieppel (11), we refrained from adding new characters to the data matrix used by the latter authors. Instead we checked in the data matrix of Lee (43) for characters that would appear relevant to a more extensive, global analysis but that were not included by deBraga & Rieppel (11). Three characters are of potential importance (numbers in accordance with Ref. 43): [5] exoccipital lateral flange absent (0), or present (1); [104] lateral pubic process absent (0), or present (1); [105] median pubic process absent


Carboniferous
Permian
Triassic
Period
Late
Early
Late
Early
Middle
Late
Moscovian
Kasimovian
Gzhelian
Asselian
Sakmarian
Artinskian
Kungurian
Ufimian
Kazanian
Tatarian
Scythian
Anisian
Ladinian
Carnian
Norian
Rhaetian
Stage
315
306
302
296
290
283
277
274
272
267
250
240
235
230
220
212
208
Age Ma
Seymouriadae
Diadectomorpha
Caseidae
Ophiacodontidae
Edaphosauridae
Sphenacodontidae
Gorgonopsia
Cynodontia
Captorhinidae
Paleothyris
Araeoscelidia
Claudiosaurus
Younginiformes
Kuehneosauridae
Rhynchocephalia
Squamata
Testudines
Placodus
Cyamodus
Eosauropterygia
Choristodera
Rhynchosauria
Trilophosaurus
Archisauriformes
Prolacertiformes
Millerettidae
Acleistorhinus
Lanthanosuchidae
Macroleter
Bradysaurus
Scutosaurus
Anthodon
Procolophon
Owenetta

(0), or present (1). However, these characters are expected not to change tree topology, but only to increase the homoplasy index because all of them are found convergently in pareiasaurs and saurians. For example, the derived state for character 5 is found not only in turtles and pareiasaurs, but also in crocodilians, eosauropterygians, and in lizards where the exoccipital is not (yet) fused to the opisthotic.

CLADISTIC ANALYSIS

As in the original analysis (11), two most parsimonious trees (MPTs) were found (a single unresolved trichotomy within archosauromorphs) with a *T*ree *L*ength (TL) of 793 steps, a consistency index (CI) of 0.503, and a *H*omoplasy *I*ndex (HI) of 0.731 (search procedures as in the original analysis; characters 2, 54, 166 are uninformative; if ignored, the two MPTs have a TL = 789, CI = 0.501, and HI = 0.735). Pruning of Testudines from its position among diapsids and grafting it into parareptiles as the sister-taxon of pareiasaurs increases *T*ree *L*ength by five steps (not significant at $p \leq 0.05$ based on the Templeton test [$T_S = 562.5$, $n = 55$]. Decay analyses yielded similar results, as five extra steps were required to collapse the reptilian node that would allow turtles to shift into parareptiles. Constraining the overall pattern of relationships in PAUP, yet forcing turtles to be the sister-group of pareiasaurs (Testudines (*Bradysaurus* (*Scutosaurus, Anthodon*))) results in a single tree with a TL of 798 (TL = 794 if uninformative characters are ignored), i.e., a tree again five steps longer. If turtles are constrained to be the sister-group of pareiasaurs, but tree topology is allowed to change in all other aspects, two trees (lack of resolution confined to Lepidosauriformes) are found with a TL = 796, i.e., three steps longer than the original MPTs. However, tree topology has changed: Procolophonoids become paraphyletic in these trees, and the interrelationships of pareiasaurs change to (Testudines (*Anthodon* (*Bradysaurus, Scutosaurus*))). Finally, allowing PAUP to search for all trees that are five steps longer than the most parsimonious reconstruction (TL = 798) results in more than 1000 trees with little or no resolution.

The Consistency Index is low, although not out of line for such a large-scale analysis. More importantly, the high Homoplasy Index suggests rampant convergence. This is also indicated by relatively low bootstrap values. The bootstrap support for the node linking turtles and sauropterygians is only 53% (2000 replications). We reexamined the list of characters and concluded that many of the proposed

Figure 1 The phylogeny and temporal occurrence of Reptilia, based on the analysis discussed in the text. The tree for Reptilia is rooted on Seymouriadae, Diadectomorpha, and the synapsids. In the phylogeny, dashed lines represent ghost lineages, solid lines represent the fossil record. Arrows at the top indicate continuation of the fossil record beyond the Triassic and may lead up to extant taxa. *Open circle* at the base of the phylogeny denotes Amniota, *solid circle* denotes Synapsida, *solid square* denotes Reptilia, *solid triangle* denotes Diapsida, *asterisk* denotes Parareptilia.

primary homologies appear to be either flawed or uninformative in an analysis covering such a broad variety of taxa. We would like, therefore, to argue that rigorous evaluation of statements of primary homology is an effective way both to minimize evolutionary steps and to maximize parsimony.

STATEMENTS OF PRIMARY HOMOLOGY

The essence of all phylogenetic reconstructions of evolutionary relationships is the character data base, i.e., the identification of "characters," or "primary homologies" (13), which are then subjected to the test of congruence (54). Although the test of congruence represents the ultimate arbiter on homology (similarity due to common ancestry) versus homoplasy (independently acquired similarity), it is itself not rooted in anatomical investigation, but is designed merely to maximize congruence and hence to minimize homoplasy. A high degree of character congruence (resulting in a relatively short TL and a relatively high CI) therefore says nothing about the quality of the character data base. Similarly, the sheer number of characters is not going to improve the quality of a phylogenetic analysis unless every one of these characters is founded in careful anatomical comparison.

The test of congruence critically depends on the rigorous application of the "test of similarity" (54) in the identification of primary homologies. The establishment of "similarity" (in terms of equivalence of topographic relations, or connectivity) may be difficult if organisms of highly derived anatomy such as turtles have to be dealt with. In such cases, the analysis of ontogenetic development, as well as comparison of organisms (fossil and extant) in terms of hypothetical transformation series in search for intermediate conditions of form, may play a crucial role in the identification of primary homologies (59). In this section we explore the importance of detailed anatomical comparison for four selected character complexes that have played a prominent role in recent discussions of turtle relationships: the dermal armor, the acromion process on the scapula, the astragalus-calcaneum complex, and the hooked fifth metatarsal. These examples are chosen for the following reasons: dermal armor and the acromion process on the scapula have been used as synapomorphies uniting pareiasaurs and turtles, but closer anatomical comparison reveals a flawed basis for the identification of primary homologies. Conversely, detailed anatomical comparison supports the astragalus-calcaneal complex and the hooked fifth metatarsal as potential homologies of turtles and diapsids on the basis of close developmental and structural correspondence.

Dermal Armor

Lee (41–43) considered the presence of a heavy dermal armor a synapomorphy of turtles and pareiasaurs, some of which show interlocking osteoderms lying closely above the vertebral column and ribs. As he believed developmental evidence indicated a primarily dermal nature of the carapace in turtles, Lee suggested that the turtle carapace developed by fusion of ancestral osteoderms. Turtles are unique among amniotes in that the scapular blade lies at a morphological level deep (ventral) to the ribs, which according to Lee (39, 40) would have resulted from a backward shift of the shoulder girdle.

The primary homology and potential synapomorphy of pareiasaur osteoderms and the turtle "dermal" armor is problematic because of the morphological complexity of the turtle carapace. The latter is recognized as a composite structure, involving "thecal" as well as "epithecal" ossifications (77, 81, 34). The thecal ossifications comprise a central longitudinal row of neurals overlying and fused to the neural arches of dorsal vertebrae, a lateral row of costal plates associated with the dorsal ribs, a marginal row of marginals, an anterior nuchal, and a posterior pygal. Epithecal ossifications are osteoderms superimposed on thecal ossifications (81, 82). It had been claimed (29, 51) that epithecal ossifications are primitive for turtles and would have covered the body of the ancestral turtle prior to the development of a theca. If so, the turtle shell could easily be derived from fused ancestral osteoderms. However, epithecal elements ossify later than thecal components during ontogeny in living turtles, and mapping the occurrence of epithecal ossifications on a cladogram of Testudines indicates their derived nature. Whereas the genuinely dermal nature of the marginal, supramarginal (*Proganochelys*—15), nuchal, and pygal plates is generally accepted (34, 75–77), the nature of the neural and costal plates remains controversial.

The basic distinction of turtles from other amniotes is not a (posterior) shift of the pectoral girdle (scapula) to a level medial (ventral) of the ribs, but a "deflection" of the ribs to a position dorsal (lateral) to the scapula (71). The carapacial ridge redirects the migration of those somitic cells that will eventually form the ribs (7), such that the ribs chondrify in a position dorsal to the scapula and within the dermal carapacial disc. Completion of perichondral ossification of the ribs shows that these are not expanded in turtles (34) at the cartilaginous stage (Figure 2). Ossification of the costal plates proceeds by the formation of trabecular bone starting from and remaining in continuity with the periost of the rib (34).

The fact that the developing ribs and neural arches pierce the dermal carapacial disc renders the identification of neurals and costals as endoskeletal versus exoskeletal elements difficult. However, endo-versus exoskeletal cannot be distinguished on the basis of histogenesis but must be defined with reference to a phylogenetic framework (53, 73). Exoskeletal elements are elements homologous to structures, which in the ancestral condition combine bone, dentine, and enamel, i.e., develop at the ectoderm-mesoderm interface. Endoskeletal elements are elements that in the ancestral condition are preformed in cartilage, while the cartilaginous stage may be deleted in the descendant (membrane bone). The neural and costal plates ossify from, and in continuity with, the periost of their endoskeletal component. This pattern of ossification corresponds to the definition of *Zuwachsknochen* given by Starck (73:13). As such, neural and costal plates are endoskeletal components of the turtle carapace and cannot be derived from a hypothetical ancestral condition by fusion of exoskeletal osteoderms.

Following this analysis of primary homology, the turtle carapace is unique, i.e., autapomorphic for turtles, and morphogenetically very distinct even from its closest counterpart among other amniotes, which is the carapace of cyamodontoid

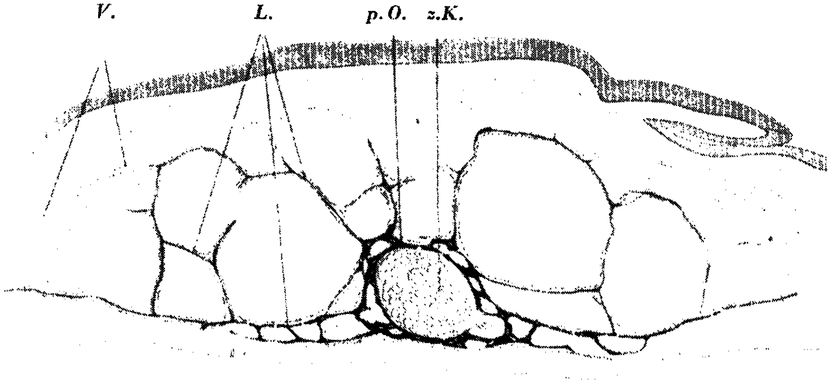


Figure 2 Cross-section through the sixth rib of an embryo of *Podocnemis unifilis*, showing the trabecular bone of the costal plate developing in continuity with the periost of the rib (from Ref. 34, with permission of S. Karger Publ.).

placodonts. The latter is composed of a mosaic of (exoskeletal) osteoderms, which may or may not be closely associated with the underlying endoskeleton (vertebrae and ribs), but which never incorporates endoskeletal elements (80).

The Acromion

The endoskeletal pectoral girdle of turtles is a triradiate structure of a highly specialized nature. The scapula forms a dorsal process with a ligamentous attachment to the anterior border of the first rib and the adjacent carapace. The coracoid forms a posteroventral process, while a medioventrally directed process of the scapula establishes a ligamentous connection to the entoplastron (78, 79). Because the ventromedial scapular process is shorter in *Proganochelys* (15) than in extant turtles, Goodrich (24) considered it an acromion. Lee (41, 43) considered the acromion a primary homology synapomorph in pareiasaurs and turtles, a conjecture of similarity rejected by deBraga & Rieppel (11).

Although it ossifies from a separate ossification center (61), it is in continuity with the scapula at the cartilaginous as well as at the fully ossified stage of its development, which suggests that the "acromion" of turtles is a process of the scapula. However, the medioventral scapular process of *Proganochelys*, homologous to the "acromial" process of modern turtles (Figure 3), fails the test of similarity with the acromion of pareiasaurs and therapsids. Both in therapsids and in pareiasaurs, the acromion is located at the dorsal tip of the clavicle, whereas the "acromion" of turtles is near the base of the clavicle and medial to it (*Proganochelys*). The "acromion" process in turtles is a medioventral extension of the scapula, not an anterolateral extension as is the acromion of pareiasaurs and nonmammalian therapsids. This difference of orientation also results in different muscle attachments

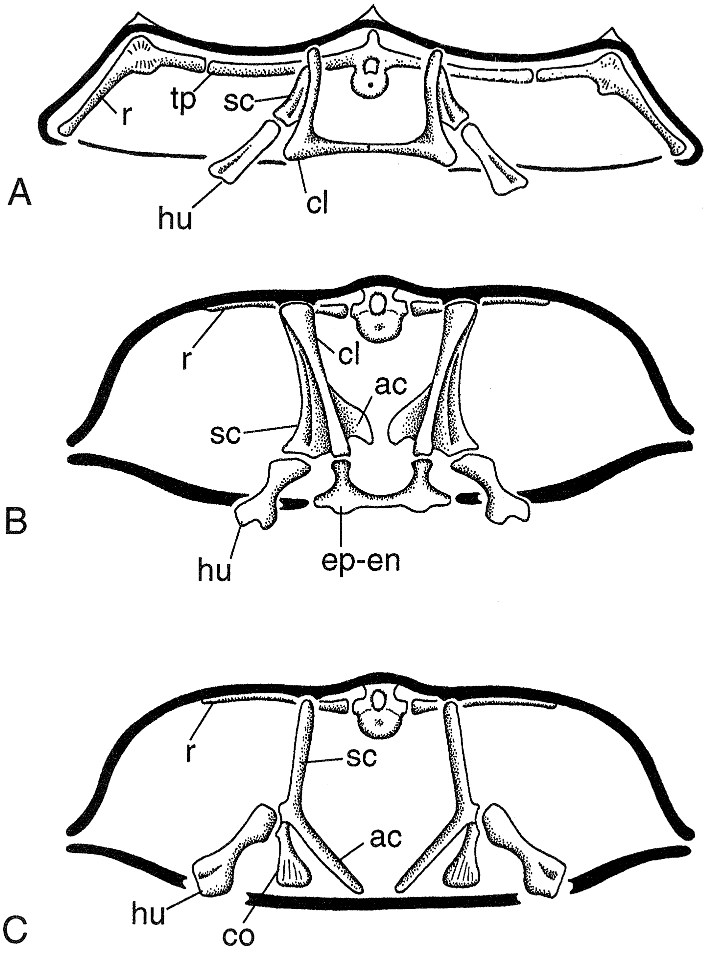


Figure 3 Schematic representation of the relation of the pectoral girdle to the dermal armor in the cyamodontoid placodont *Henodus* (A; coracoid not known), in *Proganochelys* (B; coracoid not shown as it is positioned perpendicular to the plane of the drawing), and in modern turtles (C). Abbreviations: ac, "acromion" process; cl, clavicle; co, coracoid; ep-en, epiplastron-entoplastron; hu, humerus; r, rib; sc, scapula; tp, transverse process.

(78). The fact that the "acromial" process is shorter in *Proganochelys* than in other turtles may indicate that it evolved within the clade. The ligamentous attachment of the "acromion" process to the entoplastron suggests a function in locomotion (78).

The sprawling gait primitively found in reptiles results in two principal reaction forces at the shoulder joint: a vertical component that is absorbed by the scapula and its muscular suspension from the axial skeleton, and a medially directed component that is absorbed by the clavicular-interclavicular complex. In turtles, the clavicles and interclavicle are incorporated in the plastron, and while the vertical component is absorbed by the scapula and the carapace, the medially directed force component is absorbed by the "acromion" process and the plastron (79). In *Proganochelys*, the complex epiplastra carry elongate dorsal (clavicular) processes that articulate with the dorsal process of the scapula. It is likely that medially directed forces were partly deflected from the scapula to the epiplastron-entoplastron complex via the clavicular process.

The Astragalo-Calcaneal Complex

Amniota reduce the proximal tarsal ossifications to an astragalus and a calcaneum. The astragalus is believed to have evolved by fusion of the ancestral intermedium, tibiale, and proximal centrale, whereas the calcaneum represents the ossified fibulare (55, 62). Lee (41, 43) considered the ontogenetic fusion of the astragalus and calcaneum a synapomorphy of pareiasaurs and turtles. However, an ontogenetic fusion of the astragalus and calcaneum is also observed in lepidosaurian diapsids. Secondarily marine clades, subject to skeletal paedomorphosis, may retain separate astragalus and calcaneum, as do marine turtles (77), and sauropterygians. The use of fusion of the astragalus and calcaneum in adult turtles and pareiasaurs as a synapomorphy of the two groups does not account for morphological complexity, which results from an ontogenetic repatterning of the development of the tarsus in turtles and those diapsids that develop a mesotarsal joint.

The development of the tarsus of turtles is subject to a truncation of the preaxial series (6), such that no true tibiale, connected to the tibia, forms in this group. Originally separate precartilaginous precursors in the proximal tarsus (fibulare, intermedium, and centrale), all fuse into a single block of cartilage, the "*astragaloscaphoideum*" of Gegenbaur (22), or "*tritibiale*" of Rabl (57), or "*tarsale proximale*" of Sewertzoff (72). The astragalus and calcaneum each ossify from a single ossification center within the proximal tarsal cartilage; the ossification of the astragalus precedes that of the calcaneum, and its first appearance is in an intermedium position. A third center of ossification may variably appear distal to the astragalus within the proximal tarsal cartilage of turtles, giving rise to a centrale, an element absent in *Proganochelys* (15). The development of a proximal block of cartilage in the tarsus makes it impossible for the perforating artery (84) to pass between astragalus and calcaneum, as it does in the primitive condition (62), and it accordingly shifts to a position proximal to the astragalus, passing between the distal heads of the tibia and fibula. A developmental pattern similar to that of extant turtles may be inferred for *Proganochelys*, not only because of the detailed similarity of the astragalo-calcaneal complex, but also because *Proganochelys* lacks a perforating foramen between astragalus and calcaneum (15).

The tarsus of lepidosaurian diapsids (*Sphenodon*, squamates) develops in an identical manner (although the proximal centrale is always absent in this clade). The separate precartilaginous precursors of the proximal tarsal elements again fuse to form a single proximal tarsal cartilage, within which the astragalus and calcaneum ossify from separate ossification centers (1, 22, 31, 72), and the astragalus and calcaneum fuse in the adults. The perforating artery passes proximal to the tarsal cartilage, between the distal ends of tibia and fibula (50). No fossil lepidosaur is known that has separate astragalus and calcaneum ossifications enclosing between them a foramen for the perforating artery.

Ontogenetic repatterning of the proximal tarsus in turtles and lepidosaur reptiles results in the cartilaginous preformation of the mesotarsal joint in cartilage, between the proximal tarsal cartilage and the distal tarsal 4. That way, the mesotarsal joint is fully functional in hatchlings and later growth stages. But whereas the astragalus and calcaneum also fuse in adult pareiasaurs, there is no indication of ontogenetic repatterning of the tarsus. A foramen for the perforating artery is retained within the astragalo-calcaneal complex, there is no indication of a mesotarsal joint in pareiasaurs, and the astragalo-calcaneal complex retains the primitive amniote configuration (except for its fusion) in that it is much more plate like, much broader proximo-distally, and more horizontally positioned than that of turtles and lepidosaurs.

The Hooked Fifth Metatarsal

A hooked fifth metatarsal is present in turtles (including *Proganochelys*—15), in the diapsid *Youngina* (25), as well as in the lepidosauromorph and archosauromorph clades, collectively referred to as Sauria, but it is absent in pareiasaurs or procolophonoids. Lee (45) uses arguments based on parsimony to treat the hooked fifth metatarsal of turtles and diapsids as convergent and, based on the (presumed) absence of a hooked fifth metatarsal in basal lepidosauriforms (kuehneosaurs), also considers the lepidosaurian and archosauromorph hooked fifth metatarsal as convergent (21).

The development of the hooked fifth metatarsal is identical in all three extant groups where it occurs (60, 61, 63), in that it is severely delayed in ossification in comparison to other metatarsals. If well developed (reduced in *Alligator*), perichondral ossification starts at the angulation on the medial (preaxial) side, where the hooked fifth metatarsal articulates with the proximal head of the fourth metatarsal (in contrast to other metatarsals, which show the normal mid-diaphyseal ossification). The only difference in the development of the fifth metatarsal in turtles and archosauromorphs on the one hand, and lepidosaurs on the other, is the ossification of separate epiphyses or apophyses in the latter group, adding to the complexity of the fully formed hooked fifth metatarsal in lepidosaurs (69). Ossification of epiphyses is an autapomorphy of Lepidosauria (28), and hence it is uninformative for phylogenetic inference.

Among nonlepidosaur lepidosauriforms, i.e., kuehneosaurs, the hind feet remain unknown for *Icarosaurus* (10). *Kuehneosaurus* is known from fully disarticulated material only (68), and the presence or absence of a hooked fifth metatarsal must remain conjectural. Sauropterygians, nested within saurians (64, 48), lack a hooked fifth metatarsal. Given its presence in the outgroup of saurians, *Youngina*

(25), the absence of a hooked fifth metatarsal in sauropterygians is likely due to skeletal paedomorphosis, as is also the case in marine turtles (*Dermochelys*; 77). A hooked fifth metatarsal thus represents a synapomorphy of *Youngina* plus saurians (37), including turtles, unless congruence of other characters would indicate that turtles are nested within parareptiles.

The foot of a generalized lepidosaur is strongly asymmetrical, digit length increasing from digit I through digit IV. During the initial phase of pedal plantarflexion, the metatarsus rotates around its long axis at the mesotarsal joint, such that subsequent extension of the ankle joint moves the proximal end of the metatarsus anteriorly and laterally. The fourth digit rolls off the substrate first during extension of the ankle, but digits I through III remain in contact with the substrate until the end of the propulsive phase. During this locomotor cycle, the hooked fifth metatarsal acts as a dual lever for different muscle action, once with respect to the rotation of the metatarsus around its long axis, then with respect to the extension of the ankle joint (4, 5).

In turtles, including *Proganochelys* (15), the digits are much more symmetrical in their relative length. The excursion range of (humerus and) femur retraction is somewhat restricted as compared to squamates. Initially, in turtles, during retraction of the femur, all toes point anteriorly. Toward the end of the retracting cycle, the foot performs a distinct "heel swing" that turns the heel medially around the toes, which at this time act as a pivot and which point laterally after completion of the heel swing (78, 85). In contrast to squamates, there is little plantar flexion at the end of the retractive phase. The foot is moved forward with its sole facing the substrate; its heel as well as longer claws may drag during initial phases of protraction (78). Locomotion is slower and less sophisticated in turtles compared to squamates, yet the pes of turtles shares with that of squamates a well-developed mesotarsal joint as well as a hooked fifth metatarsal. This suggests that these latter features were inherited by turtles from their common ancestor, rather than developed within turtles in convergence to squamates, a conclusion supported by our phylogenetic analysis.

THE PHYLOGENETIC INFORMATION CONTENT OF MORPHOLOGICAL CHARACTERS

The modified global analysis used to evaluate turtle relationships is based on a data matrix characterized by an unusually large number of homoplastic characters that are not useful in resolving relative relationships, whereas a relatively small and different set of characters defines the observed topology. We expected that those characters that cause the high Homoplasy Index would be clustered in certain parts of the anatomy, such as the locomotory system, and could therefore be related to some functional trends seen in amniotes. For example, the evolution of Paleozoic amniotes appears to involve the gradual change from a locomotor system that relies primarily on lateral undulation of the vertebral column for propulsion, to one that can be described as a combination of limb-driven locomotion with lateral undulation. This evolutionary innovation has been achieved independently within several amniote clades and necessitates changes in the shoulder girdle, propodials, metapodials, and phalanges to allow for increasing stride length. This phenomenon could be viewed as an evolutionary arms race at the predator-prey level, involving forms that coexisted but were not closely related (pareiasaurs and carnivorous therapsids, for example). However, in our analysis the homoplastic (convergent) characters are distributed randomly throughout the skeleton.

Convergent characters affect the skull roof pattern: 6, 11, 17(1), 20, 38, 55; braincase: 66, 68; palate: 75, 76(1), 77, 78, 79; mandible: 83(1), 85, 86, 87, 91, 92; axial skeleton: 110, 111; appendicular skeleton: 115, 130, 144, 149, 150, 153, ?158, 160.

Examination of convergent cranial features (the derived condition appearing convergently in parareptiles, diapsids, turtles, and often also in derived synapsids) suggests that certain morphological transformations cannot convey a phylogenetic signal at the taxonomic level addressed by the evaluation of turtle relationships. The shape and orientation of nares [6], the shape and size of the lacrimal bone [17], the loss of bones such as the tabular [55], and the shape of particular palatal bones [75, 76, 77, 79] evolved independently several times within amniotes. However, the same characters may still be useful in evaluating patterns of relationships within more restricted clades of amniotes. The shape and size of the lacrimal bone, for example, provides important phylogenetic information within basal synapsids or within basal parareptiles (38).

Similarly, palatal characters such as the shape and size of the pterygoid [76, 77, 78, 79] may be associated with reduction and/or loss of palatal dentition, an evolutionary event that occurred independently in several clades, including derived synapsids, lepidosaurs, and some parareptiles. Several convergent mandibular characters may be associated with changes of insertion of jaw closing [83, 85, 86, 87, 91] and jaw opening [92] muscles.

In addition, larger analyses generally tend to have a progressively smaller Consistency Index, a progressively higher Homoplasy Index, and the resulting pattern of relationships tends to be rather weakly supported. The resolution of the above pattern of relationships is based on a relatively small number of characters within a much larger data set. Ultimately, the number of synapomorphies supporting a diapsid-turtle relationship outnumbers those that support a parareptile-turtle pattern. Yet a significant number of characters (listed above) appear to remain uninformative as relative relationships are analyzed across a broad range of taxa that have dramatically different body designs. We would like to argue for the need to reconsider the phylogenetic signal provided by morphological features at different levels of inclusiveness, and we would also like to point out that larger is not necessarily better when considering the size of data matrices in large-scale phylogenetic analyses.

EVOLUTIONARY SCENARIOS, PHYLOGENIES, AND CONVERGENCE

A case has recently been made that evolutionary scenarios, if based on independent evidence, should be allowed to provide the basis for choice among several equally parsimonious phylogenetic hypotheses, or even to overturn weakly supported cladograms (46). Independent evidence for evolutionary scenarios is to be derived from genetic, developmental, and/or functional correlation. We believe this claim to be flawed, because hypotheses of character correlation can only be tested by reference to a phylogeny. To import evolutionary scenarios into phylogeny reconstruction results in an empirically empty research program. By contrast, in a case such as turtle interrelationships, with competing yet vastly different phylogenetic hypotheses, the question can be asked, which one of the alternative hypotheses of turtle relationships better supports a plausible and parsimonious evolutionary scenario of turtle origins.

Lee (39, 40, 42) argued in favor of a gradual transition from terrestrial and herbivorous pareiasaurs to a turtle body plan. Shortening of the trunk, a shift from axial to paraxial locomotion, broadening of the ribs, fusion of osteoderms above the ribs to form a carapace, ankylosis of the vertebrae underlying the carapace, and a posterior migration of the shoulder girdle are considered essential steps in that transition. Here we argue that Lee's (39, 40, 42) scenario of turtle origins by "correlated progression" greatly oversimplifies the evolutionary changes that took place in the origin of the turtle body plan, and that functional constraints discussed below render it unlikely that turtles had a terrestrial origin.

Our phylogenetic hypothesis cannot resolve the question of whether the hypothetical common ancestor of turtles and sauropterygians was aquatic or terrestrial. If turtles are coded polypmorphic for terrestrial and/or aquatic habits, optimization shows this character to be equivocal at the node uniting turtles and sauropterygians. If turtles are coded terrestrial, their origin becomes unequivocally terrestrial; if they are coded aquatic, their origin becomes unequivocally aquatic. *Proganochelys* was reconstructed as an aquatic bottom walker on the basis of limb proportions, but some characters such as the elephantine feet, the high domed shell, and the heavy armor suggest terrestrial habits as well (15). By contrast, functional constraints implicit in the evolution of the turtle body plan would seem to suggest an aquatic origin for the clade.

There is no broadening of the ribs in turtles, and the carapace cannot be derived from a simple fusion of osteoderms. Although a slight posterior shift of the shoulder girdle sems to have occurred in turtles (8), the position of the scapula inside the rib cage is primarily the result of a deflection of rib growth to a more superficial position (7, 71). As the ribs become part of costal plates, and the tips of the neural arches expand to form neurals, complete ossification of the carapace fully immobilizes the dorsal vertebral column. The neural arches of turtles move forward by half a segment in the dorsal region, carrying the ribs with them (23). As a result, the proximal heads of the ribs are positioned intrasegmentally (with respect to the primary segmentation of the paraxial mesoderm), i.e., on the boundary between successive centra (assuming these form by resegmentation as in other amniotes). Likewise, the neural arches bridge the boundaries between successive centra, and in marine turtles subject to skeletal paedomorphosis, the neural arches can be seen to meet each other in a suture located above the midpoint of the dorsal centra. At this level, the two successive neural arches together with the centrum enclose the opening for the exit of the spinal nerve, which hence comes to lie intersegmentally. In other turtles, the dorsal neural arches fuse with one another to form a vertical blade, the "neural spine" (30), pierced by the spinal nerves at an intersegmental level. The myomeric and neuromeric segmentation is secondarily established in the dorsal region of turtles, as was already the case in *Proganochelys* (15). Intercostal muscles atrophy during embryonic development (23).

As a consequence of dramatic restructuring in the evolution of the turtle body plan, the ribs lose their function in support of respiration and locomotion. In a generalized tetrapod reptile, aspiration of air is effected by an expansion of the body cavity through muscular action exerted on the ribs. Exhalation is effected either by passive recoil of the body walls, and/or by compression of the lungs as a result of active compression of the rib cage. By contrast, respiration in turtles depends on volume changes of the thoracico-peritoneal cavity inside the rigid dermal armor, which is achieved by altering the position of the limb flanks through the activity of anterior and posterior muscles (18). A comparison of respiration in an aquatic (*Chelydra*) and a terrestrial (*Testudo*) turtle resulted in the identification of three forces that influence the relative volume of the thoracico-peritoneal cavity: These forces are muscular activity, gravity (supporting inhalation), and, in aquatic turtles, hydrostatic pressure (supporting exhalation) (19). Experimental analysis of muscle activity during breathing in *Chelydra* as compared to *Testudo* showed an adjustment of inhalatory and exhalatory muscle output to hydrostatic pressure in the aquatic turtle, the generated forces generally approaching a minimum. At the limit, both inhalation and exhalation may be passive in the aquatic environment, powered by gravity and hydrostatic pressure, respectively (19). Furthermore, both terrestrial and aquatic turtles show a much higher degree of tolerance of anoxia as compared to crocodiles or squamates (2). Collectively, these data suggest that the transition to the mode of respiration characteristic of turtles would be easier to achieve in an aquatic than in a terrestrial environment.

In terrestrial reptiles, body weight is transferred from the shoulder girdle (scapula) to the axial skeleton by means of a muscular sling, principally the *serratus ventralis*. Its probable homologue in turtles is the *testocoracoideus* muscle, which participates in the expansion of the thoracico-peritoneal cavity and hence supports inhalation (18, 19, 78). It would seem difficult to simultaneously derive the turtle mode of respiration and locomotion in a terrestrial environment that requires continuous body support. By contrast, the aquatic environment provides buoyancy, which greatly facilitates both body support and locomotion. The initial integration of the clavicular-interclavicular complex into the plastron, and the concomitant development of an acromion process on the scapula to absorb medially directed forces generated by limb movements, would appear to be easier to achieve in an aquatic environment for a bottom-walking turtle supported by some degree of buoyancy, more than in the terrestrial environment.

The development of a plastron in itself indicates an aquatic origin of turtles, as it provides dermal protection for the ventral body surface, which in terrestrial tetrapods is not immediately exposed to predatory impact. Indeed, the only other amniotes that evolved a plastron joined to a carapace by a bridge covering the lateral body wall are derived members of marine cyamodontoid placodonts (27). Although superficially very similar, the dermal armor of cyamodontoids is convergent upon that of turtles (see discussion above). However, such a striking case of convergence could be considered to lend additional support, by analogy, to the hypothesis of an aquatic origin of turtles. In addition to protection, both groups may have developed extensive dermal armor as an osmotic barrier. Experimental studies have shown a significantly smaller rate of gain of water (in fresh water) or loss of water (in sea water) in a slider turtle (*Trachemys scripta*) with a well-ossified carapace and plastron, as opposed to a soft-shelled turtle (*Apalone spiniferus*) or a caiman (*Caiman crocodilus*) (3). The function of the dermal armor as an osmotic barrier may explain why cyamodontoid placodonts were the last stem-group sauropterygians to go extinct at the end of the Triassic, as shallow epicontinental and nearshore marine habitats deteriorated in the wake of an eustatic sea-level drop. *Henodus* for example persisted under extreme environmental conditions in a lagoonal lake environment that oscillated between rain flooding and hypersalinity (14). The function of the dermal armor as an osmotic barrier may also explain the diversity and wide geographic distribution in a broad range of habitats of early fossil occurrences of turtles as detailed below.

The scenario of an aquatic origin of turtles is in accordance with the occurrence of the earliest known fossil turtle in the shallow epicontinental marine deposits of the Germanic Muschelkalk (Middle Triassic, lower Ladinian, 235 mys; R Wild, personal communication). The occurrence of a proganochelyid turtle in marine deposits indicates that this clade of early turtles, if not including marine members, at least pursued an amphibious mode of life, living in delta systems or lake systems close to the sea shore; fully terrestrial animals are not expected in Muschelkalk deposits. The same general type of habitat is indicated for the geologically younger occurrences of *Proganochelys quenstedti* in the Upper Triassic (middle Norian) Stubensandstein (15).

The occurrence of the earliest fossil turtle, as well as of *Proganochelys*, in the Germanic Triassic (i.e., in the western Tethyan faunal province) also matches paleobiogeographic patterns. Triassic Sauropterygia, sister-group of Testudines, comprise two major clades, the Placodontia and the Eosauropterygia (64). Of these, the Placodontia are of strictly western Tethyan distribution. Eosauropterygia have their earliest occurrences in the uppermost Lower Triassic (Scythian) of the Germanic Basin (western Tethyan faunal province), of southern China (western Pacific faunal province), and in the western United States (eastern Pacific faunal province). Throughout the Middle Triassic, the western Tethyan faunal province was a center of diversification for stem-group Sauropterygia (67). By Upper Triassic times, the diversity of stem-group sauropterygians declines, while turtles are found in the Upper Triassic of Thailand (12), of Greenland (33), and of Argentina (70). Lower Jurassic turtles are known from northeastern Arizona (17) and from South Africa (16). This shows that during Late Triassic and Early Jurassic times, a substantial radiation of turtles took place at a cosmopolitan scale, some of the clades adopting a fully terrestrial mode of life in an arid environment (16).

The hypothesis of a sauropterygian sister-group relationship of turtles furthermore closes an important gap in the fossil record. Large amounts of tetrapod material have been collected from the Permian of Russia, South Africa, and North America, but not one single turtle carapace fragment. Given that pareiasaurs arise in the lower-most part of the Upper Permian (*Tapinocephalus* zone—36), the origin of turtles would have to date back to the Lower Permian if turtles and pareiasaurs are sister taxa (41), leaving a gap of over 30 million years between the origin and the first fossil occurrence of turtles. However, if Lee (43) is correct and turtles are nested within Pareiasauria as the sister-group to his Fleocyclopsia (including the late Permian pareiasaur *Anthodon*), turtles might have originated at the end of the Upper Permian, which still leaves a gap of about 15–20 million years. Molecular data, which also support diapsid affinities of turtles, indicate an age of 207 ± 20.5 Ma for the turtle lineage (29a) bringing them closer to the Middle Triassic diversification of Sauropterygia. Admittedly, this argument is based on negative evidence, i.e., the absence of turtles in the late Paleozoic fossil record, but the cosmopolitan distribution of turtles by Upper Triassic times does indicate that once turtles are present in a fauna, their carapace, or fragments thereof, stand a reasonably good chance to fossilize.

CONCLUSIONS AND FUTURE PERSPECTIVES

It is intuitively difficult to accept a sister-group relationship of turtles with Sauropterygia among crown-group diapsids, even for the authors of this paper. Yet this is what the osteological data at hand do indicate at this time. As a cautionary note, we would like to emphasize that removal of Sauropterygia from the phylogenetic analysis discussed above results in the movement of turtles into parareptiles, as the sister-group of pareiasaurs (with paraphyletic procolophonians). This indicates that inclusion of Sauropterygia did have a significant effect on the placement of turtles among diapsids. Bootstrap support for the node linking turtle to sauropterygia is weak (53%). The question could be raised whether the turtle-sauropterygian relationship picks up aquatic adaptations in those two groups, rather than a phylogenetic signal? However, the synapomorphies nesting turtles within crown-group Diapsida are distributed throughout the skeleton (11) and cannot readily be linked to aquatic adaptations. The addition of ichthyosaurs, a group of dolphin-like Mesozoic aquatic reptiles, to the data matrix of deBraga & Rieppel (11) again appears to switch turtles back into parareptiles (49). Although we do not anticipate the same result if ichthyosaurs were added to the data matrix in its current corrected form, it certainly is a hypothesis that has to be tested. Thalattosaurs is another group of marine reptiles that may represent the sister-group of Sauropterygia (48), with turtles being the sister-taxon of these two clades (65), but knowledge of thalattosaur anatomy is presently very incomplete, and relative relationships may change once thalattosaurs become more fully known.

Beyond the addition of new taxa, and also of new osteological data to the analysis, there is an obvious need for further testing the three-taxon problem involving Lepidosauria, Archosauria, and Testudines on the basis of other, perhaps also less conventional, characters of molecular and/or physiological nature. Recent contributions (29a, 35, 56, 83) have provided interesting support for turtles as diapsids. It is striking how little comparative physiological work has been done on turtles in a phylogenetic context compared to lizards (32). Although hampered by the relative lack of outgroups when compared to paleontological sources, molecular and physiological studies have the potential to contribute significantly to our understanding of turtle origins and relationships.

We remain convinced that phylogenetic analyses with incorporation and integration of new data not only from paleontological sources, but also neontological sources when relevant (gross morphology, ontogenetic, molecular, physiological), provide the best line of investigation for evaluation of the evolutionary history of amniotes and the origin of turtles.

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LITERATURE CITED

1. Baur G. 1885. Zur Morphologie des Carpus und Tarsus der Reptilien. *Zool. Anz.* 8:631–38
2. Bennett AF, Dawson WR. 1976. Metabolism. In *Biology of the Reptilia*, ed. C Gans, WR Dawson, 5:127–223. London: Academic
3. Bentley PJ. 1976. Osmoregulation. In *Biology of the Reptilia*, ed. C Gans, WR Dawson, 5:365–412. London: Academic
4. Brinkman D. 1980. Structural correlates of tarsal and metatarsal functioning in *Iguana* (Lacertilia; Iguanidae) and other lizards. *Can. J. Zool.* 58:277–89
5. Brinkman D. 1981. The hind limb step cycle of *Iguana* and primitive reptiles. *J. Zool.* 181:91–103
6. Burke AC, Alberch P. 1985. The development and homologies of the chelonian carpus and tarsus. *J. Morph.* 186:119–31

7. Burke AC. 1989. Development of the turtle carapace: implications for the evolution of a novel bauplan. *J. Morph.* 199:363–78

8. Burke AC. 1991. The development and evolution of the turtle body plan: inferring intrinsic aspects of the evolutionary process from experimental embryology. *Am. Zool.* 31:616–27

→ Carroll RL. 1969. A Middle Pennsylvanian captorhinomorph, and the interrelationships of primitive reptiles. *J. Paleontol.* 43:151–70

10. Colbert EH. 1970. The Triassic gliding reptile *Icarosaurus*. *Bull. Am. Mus. Nat. Hist.* 143:85–142

11. deBraga M, Rieppel O. 1997. Reptile phylogeny and the interrelationships of turtles. *Zool. J. Linn. Soc.* 120:281–354

12. deBroin F. 1984. *Proganochelys ruchae* n. sp., chélonien du Trias supérieur de Thailande. *Stud. Geol. Salamanticensia-Stud. Palaeocheloniológica* 1:87–97

13. dePinna MCC. 1991. Concepts and tests of homology in the cladistic paradigm. *Cladistics* 7:367–394

14. Fischer W. 1959. Neue Funde von *Henodus chelyops* v. Huene im Tübinger Gipskeuper. *N. Jb. Geol. Paläontol., Mh.* 1959:241–47

15. Gaffney ES. 1990. The comparative osteology of the Triassic turtle *Proganochelys*. *Bull. Am. Mus. Nat. Hist.* 194:1–263

16. Gaffney ES, Kitching JW. 1994. The most ancient African turtle. *Nature* 369:55–58

1 → Gaffney ES, Hutchison JH, Jenkins FA Jr, Meeker L. 1987. Modern turtle origins: the oldest known cryptodire. *Science* 237:289–91

18. Gans C, Hughes GM. 1997. The mechanism of lung ventilation in the tortoise *Testudo graeca* Linné. *J. Exp. Biol.* 47:1–20

19. Gaunt AS, Gans C. 1969. Mechanics of respiration in the snapping turtle, *Chelydra serpentina* (Linné). *J. Morph.* 128:195–228

20. Gauthier J, Kluge AG, Rowe T. 1988. Amniote phylogeny and the importance of fossils. *Cladistics* 4:105–209

21. Gauthier JR, Estes R, deQueiroz K. 1988. A phylogenetic analysis of Lepidosauromorpha. In *Phylogenetic Relationships of the Lizard Families*, ed. R Estes, G Pregill, pp. 15–98. Stanford, CA: Stanford Univ. Press

22. Gegenbaur C. 1864. *Untersuchungen zur vergleichenden Anatomie der Wirbelthiere. Erstes Heft. Carpus und Tarsus*. Leipzig: Wilhelm Engelman

23. Goette A. 1899. Über die Entwicklung des knöchernen Rückenschildes (Carapax) der Schildkröten. *Z. wiss. Zool.* 66:407–34

24. Goodrich ES. 1930. *Studies on the Structure and Development of Vertebrates*. London: Macmillan

25. Goodrich ES. 1942. The hind foot of *Youngina* and the fifth metatarsal in Reptilia. *J. Anat.* 76:308–12

26. Gregory WK. 1946. Pareiasaurs versus placodonts as near ancestors to turtles. *Bull. Am. Mus. Nat. Hist.* 86:275–326

27. Haas G. 1969. The armor of placodonts from the Muschelkalk of Wadi Ramon (Israel). *Israel J. Zool.* 18:135–47

28. Haines RW. 1969. Epiphyses and sesamoids. In *Biology of the Reptilia*, ed. C Gans, TS Parsons, AdA Bellairs, 1:81–115. London: Academic

2 → Hay OP. 1898. On *Protostega*, the systematic position of *Dermochelys*, and the morphogeny of the chelonian carapace and plastron. *Am. Nat.* 32:929–48

2 → Hedges SB, Poling LL. 1999. A molecular phylogeny of reptiles. *Science* 283:998–1001

30. Hoffstetter R, Rage J-C. 1969. Vertebrae and ribs of modern reptiles. In *Biology of the Reptilia*, ed. C Gans, TS Parsons, AdA Bellairs, 1:201–310. London: Academic Press

31. Howes GB, Swinnerton HH. 1901. On the development of the skeleton of the Tuatara,

Sphenodon punctatus; with comments on the egg, the hatching, and the hatched young. *Trans. Zool. Soc. Lond.* 16:1–86

32. Huey RB. 1987. Phylogeny, history, and the comparative method. In *New Direction in Physiological Ecology*, ed. ME Fered, AF Bennett, WW Burggren, RB Huey, pp. 76–98. New York: Cambridge Univ. Press
33. Jenkins FA Jr. 1994. Late Triassic continental vertebrates and depositional environments of the Fleming Fjord Formation, Jameson Land, East Greenland. *Medd. Gronl. Geosci.* 32:1–25
34. Kaelin J. 1945. Zur Morphogenese des Panzers bei den Schildkröten. *Acta Anat.* 1:144–76
35. Kirsch JAW, Mayer GC. 1998. The platypus is not a rodent: DNA hybridization, amniote phylogeny and the palimpsest theory. *Philos. Trans. R. Soc. Lond. B* 353: 1221–37
36. Kitching JW. 1977. *The Distribution of the Karroo Vertebrate Fauna*. Bernard Price Inst. for Palaeontol. Res., Memoir 1. Johannesburg: Univ. Witwatersrand
37. Laurin M. 1991. The osteology of a Lower Permian eosuchian from Texas and a review of diapsid phylogeny. *Zool. J. Linn. Soc.* 101:59–95
38. Laurin M, Reisz RR. 1995. A reevaluation of early amniote phylogeny. *Biol. J. Linn. Soc.* 113:165–223

→ Lee MSY. 1993. The origin of the turtle body plan: bridging a famous morphological gap. *Science* 261:1716–20

40. Lee MSY. 1994. The turtle's long lost relatives. *Nat. Hist.* 6:63–65
41. Lee MSY. 1995. Historical burden in systematics and the interrelationships of 'parareptiles'. *Biol. Rev.* 70:459–547
42. Lee MSY. 1996. Correlated progression and the origin of turtles. *Nature* 379:811–15
43. Lee MSY. 1997. Pareiasaur phylogeny and the origin of turtles. *Zool. J. Linn. Soc.* 120:197–280
44. Lee MSY. 1997. Reptile relationships turn turtle. *Nature* 389:245–46
45. Lee MSY. 1997. The evolution of the reptilian hindfoot and the homology of the hooked fifth metatarsal. *J. Evol. Biol.* 10:253–63
46. Lee MSY, Doughty P. 1997. The relationship between evolutionary theory and phylogenetic analysis. *Biol. Rev.* 72:471–95
47. Maddison WP, Maddison R. 1992. *MacClade, Version 3*. Sunderland: Sinauer
48. Merck JW. 1997. A phylogenetic analysis of the euryapsid reptiles. *J. Vert. Paleontol.* 17:65A
49. Motani R, Minoura, Ando T. 1998. Ichthyosaurian relationships illuminated by new primitive skeletons from Japan. *Nature* 393:255–57
50. O'Donoghue CH. 1921. The blood vascular system of the Tuatara, *Sphenodon punctatus. Philos. Trans. R. Soc. Lond.* 210: 175–252
51. Oguschi K. 1911. Anatomische Studien an der japanischen dreikralligen Lippenschildkröte (*Trionyx japanicus*). *Morph. Jb.* 43:1–106
52. Olson EC. 1947. The family Diadectidae and its bearing on the classification of reptiles. *Fieldiana (Geol.)* 11:1–53
53. Patterson C. 1977. Cartilage bones, dermal bones and membrane bones, or the exoskeleton versus the endoskeleton. In *Problems in Vertebrate Evolution*, ed. SM Andrews, RS Miles, AD Walker, pp. 77–121. London: Academic
54. Patterson C. 1982. Morphological characters and homology. In *Problems of Phylogenetic Reconstruction*, ed. KA Joysey, AE Friday, pp. 21–74. London: Academic

→ Peabody FE. 1951. The origin of the astragalus of reptiles. *Evolution* 5:339–44

56. Platz JE, Conlon JM. 1997. Reptile relationships turn turtle ... and turn back again. *Nature* 389:245–46
57. Rabl C. 1910. *Bausteine zu einer Theorie*

der Extremitäten der Wirbeltiere. 1. Theil. Leipzig: Wilhelm Engelmann

58. Reisz RR, Laurin M. 1991. *Owenetta* and the origin of turtles. *Nature* 349:324–26
59. Remane A. 1952. *Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik.* Leipzig: Akademische Verlagsgesellschaft
60. Rieppel O. 1992. Studies on skeleton formation in reptiles. III. Patterns of ossification in the skeleton of *Lacerta vivipara* Jacquin (Reptilia, Squamata). *Fieldiana (Zool.) n.s.* 68:1–25
61. Rieppel O. 1993. Studies on skeleton formation in reptiles: patterns of ossification in the skeleton of *Chelydra serpentina. J. Zool.* 231:487–509

→ Rieppel O. 1993. Studies on skeleton formation in reptiles. IV. The homology of the reptilian (amniote) astragalus revisited. *J. Vert. Paleontol.* 13:31–47

63. Rieppel O. 1993. Studies on skeleton formation in reptiles. V. Patterns of ossification in the skeleton of *Alligator mississippiensis* Daudin (Reptilia, Crocodylia). *Zool. J. Linn. Soc.* 109:301–25
64. Rieppel O. 1994. Osteology of *Simosaurus gaillardoti*, and the phylogenetic interrelationships of stem-group Sauropterygia. *Fieldiana (Geol.) n.s.* 28:1–85
65. Rieppel O. 1998. The systematic status of *Hanosaurus hupehensis* (Reptilia, Sauropterygia) from the Triassic of China. *J. Vert. Paleont.* 18:545–76
66. Rieppel O, deBraga M. 1996. Turtles as diapsid reptiles. *Nature* 384:453–55
67. Rieppel O, Hagdorn H. 1997. Paleobiogeography of Middle Triassic Sauropterygia in Central and Western Europe. In *Ancient Marine Reptiles*, ed. JM Callaway, EL Nicholls, pp. 121–44. San Diego: Academic
68. Robinson PL. 1962. Gliding lizards from the Upper Keuper of Great Britain. *Proc. Geol. Soc. Lond.* 1601:137–46
69. Robinson PL. 1975. The functions of the hooked fifth metatarsal in lepidosaurian reptiles. *Coll. Int. CNRS* 218:461–83

→ Rougier GW, Fuente MS, Arcucci AB. 1995. Late Triassic turtles from South America. *Science* 268:855–58

71. Ruckes H. 1929. Studies in chelonian osteology. Part II. The morphological relationships between girdles, ribs and carapace. *Ann. N. Y. Acad. Sci.* 31:81–120
72. Sewertzoff AN. 1908. Studien über die Entwicklung der Muskeln, Nerven und des Skeletts der Extremitäten der niederen Tetrapoda. *Bull. Soc. Imp. Nat. Mosc. N.S.* 21:1–430
73. Starck D. 1979. *Vergleichende Anatomie der Wirbeltiere auf evolutionsbiologischer Grundlage,* Vol. 2. Berlin: Springer Verlag
74. Swofford DL, Begle DP. 1993. *PAUP–Phylogenetic Analysis Using Parsimony, Version 3.1.* Washington, DC: Smithsonian Inst.
75. Vallén E. 1942. Beiträge zur Kenntnis der Ontogenie und der vergleichenden Anatomie des Schildkrötenpanzers. *Acta Zool. Stockholm,* 23:1–127
76. Versluys J. 1914. Über die Phylogenie des Panzers der Schildkröten und über die Verwandtschaft der Lederschildkröte (*Dermochelys coriacea*). *Paläontol. Zeit.* 1:321–47
77. Völker H. 1913. Über das Stamm, Gliedmassen-, und Hautskelett von *Dermochelys coriacea* L. *Zool. Jb., Anat.* 33:431–552

→ Walker WF. 1971. A structural and functional analysis of walking in the turtle, *Chrysemis picta marginata. J. Morph.* 134:195–214

79. Walker WF. 1973. The locomotor apparatus in turtles. In *Biology of the Reptilia*, ed. C Gans, TS Parsons, 4:1–100. London: Academic
80. Westphal F. 1975. Bauprinzipien im Panzer der Placodonten (Reptilia triadica). *Paläont. Z.* 49:97–125
81. Zangerl R. 1939. The homology of the shell elements in turtles. *J. Morph.* 65:383–406
82. Zangerl R. 1969. The turtle shell. In *Biol-*

ogy of the Reptilia, ed. C Gans, TS Parsons, AdA Bellairs, 1:311–339. London: Academic

8 → Zardoya R, Meyer A. 1998. Complete mitochondrial genome suggests diapsid affinities of turtles. *Proc. Natl. Acad. Sci. USA* 95:14226–31

84. Zuckerkandl E. 1895. Zur Anatomie und Entwicklungsgeschichte der Arterien des Unterschenkels und des Fusses. *Anat. Hefte* 5:207–291

85. Zug GR. 1971. Buoyancy, locomotion, morphology of the pelvic girdle and hindlimb, and systematics of cryptodiran turtles. *Misc. Publ. Mus. Zool. Univ. Mich.* 142:1–98